Review

Fire as a pre-emptive evolutionary trigger among seed plants

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A B S T R A C T

There is mounting evidence that much of the world's vegetation has been fire-prone since the Upper Cretaceous, taking precedence over Cenozoic drought as a key agent of selection in the evolution of specialized traits adaptive to environmental stresses that otherwise result in species extinction. This raises the question of when the advent of surface fires occurred compared with the introduction of other critical selective agents, such as frost, seasonal drought, crown fire, nutrient-impoverished soils, new habitat types, and novel pollinators, herbivores and dispersal agents. Of particular interest is the relative time of origin of traits associated with fire-free habitats that traditionally have been viewed as ancestral. We collated 47 paired time sequences for a wide range of clades most of whose species are fire-prone. The objective was to determine the order of origin of fire-related traits relative to the origin of other fire-related traits associated with different fire regimes or non-fire-related traits in response to selective agents unrelated to fire. The results show that the initiation of fire-related traits in response to moderate fires (trigger 1) preceded either a) other fire-related traits that represent responses to an increase in the intensity or frequency of fire (trigger 2) (10 comparisons), b) traits associated with fire-free habitats (12 comparisons), or c) novel traits associated with selective agents unlinked to fire, with the fire-related traits now stabilized (25 comparisons). The only exception was the presence of ectomycorrhizas among pines, which are diagnostic for Pinaceae, suggesting that adaptations to poor soils occurred before this highly fire-prone genus evolved. For some early traits, there was confounding with several possible key selective agents apparently acting concurrently, although fire was always present, and these await further clarification. We conclude that fire has had a pre-emptive role in shaping many specialized traits fundamental to plant survival among fire-prone clades and that other selective agents, such as summer drought, have had a secondary role in promoting the evolution of additional novel traits that increased fitness in more recent times.

1. Introduction

The long-held view that fire is a recent phenomenon that only became a selective agent once the Earth grew increasingly dry during the Neogene is gradually being discredited (Keeley et al., 2011; Bond, 2015; He and Lamont, 2017). The key has been to establish that lineages with fire-related traits were fire-prone before they adopted these traits so that they could not be treated as adaptations to drought and merely exaptations to fire that occurred later (Lamont and He, 2017a). Together with their ability to enhance fitness in the presence of fire, this continuous association with fire means that fire-stimulated resprouting, flowering, seed release and germination may be treated as true fire adaptations. Here, establishing the sequence in which the two selective agents, fire and drought, have arisen has been paramount. We might now query where the advent of fire fitted in compared with other climatic variables (such as frost), different types of fire, nutrient-

impoverished soils, new habitat types, and introduction of novel pollinators, herbivores and dispersal agents. Compared with other likely agents of selection, fire can be expected not only to have a severe impact on fitness but to have an ongoing effect even in the presence of these other environmental constraints. Among six classes of selective agents, fire probably vies with nutrient-impoverished soils as having the greatest impact on plant fitness over geological time scales (Table 1) and hence determining when it started to drive species diversification relative to other selective agents is a central question in evolutionary ecology (Rundel et al., 2018).

Our purpose here is to establish a time sequence for the advent of environmental triggers that induce the evolution of new plant traits (Fig. 1). Using the fire-drought sequence as a model (Lamont and He, 2017a), our working hypothesis was that (mild) fire pre-empted all other selective agents in directing trait change through evolutionary time in fire-prone clades. This includes both a significant difference in

Table 1
Postulated ranking (1 = highest to 6 = lowest effect) of six common agents of selection (environmental constraints) in terms of their extent and impact over geological time scales in order to gauge the relative importance of fire (indicated by the sum of the ranks for nine properties of these selective agents). See Lamont et al. (2017a), Hu et al. (2018) and Pausas and Lamont (2018) for a discussion on the relative impacts of most of these environmental constraints on plant fitness.

| Agent of selection | Intensity | Properties of agent of selection (environmental constraint) | | | | | | | | Overall impact (Σ ranks) |
		Frequency/ persistence	Spatial coverage	Strata continuity	Horizontal continuity	Year-round effect	Mortality	Reduced fecundity	Duration of effect	
Poor soils	3	1	1	1	1	4	4	3	1	19
Fire	1	4	3	4	2	2	1	1	2	20
Drought/frost/heat	2	5	2	3	2	3	3	4	5	29
Plant-disease relations	5	3	6	2	5	5	2	2	3	33
Shade	6	4	4	6	3	1	6	5	2	37
Plant-animal relations	4	2	5	5	4	5	5	6	4	40
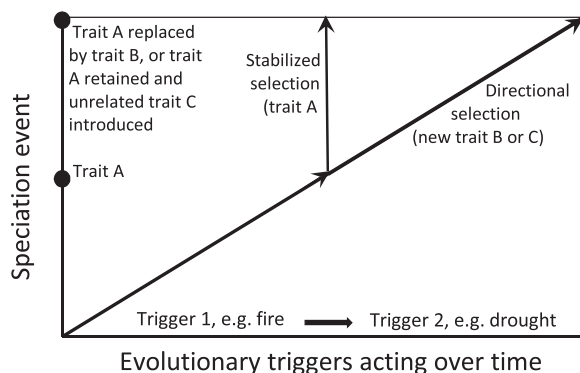
Fig. 1. Determining the sequence of evolutionary triggers in terms of sequence of trait response innovations. Thus, trigger 1 (e.g. occasional fire) promotes the evolution of trait A, followed by trigger 2 that promotes the evolution of other traits, and thus a second speciation event, that involves either the replacement of trait A by trait B adapted to a different fire regime (e.g. fires are now more intense, reach the crown and promote on-plant seed storage) or retention of trait A (stabilized selection) as it remains adaptive, with the addition of trait C unrelated to trait A, e.g. fires remain occasional but seasonal drought intensifies and leads to a new drought-adapted trait (directional selection).

the fire regime as well as the introduction of some other unrelated environmental factor. Thus, mild fire would be characterized by low flames restricted to the ground flora with minimal consumption of biomass. This contrasts with more intense or frequent fire, with the former characterized by tall flames reaching and extending beyond the canopy with extensive biomass consumption at intervals exceeding several decades, and the latter by widespread fires at < 5-year intervals consuming most of the ground cover. We identified 47 studies that included the timing of changes in non-fire-related traits and compared these with the timing of the onset of fire-related traits (usually from other studies) in that clade. Where several fire-related traits co-occurred we compared their times of origin and likely causes. These cases were grouped under five clades abundant in fire-prone regions and whose evolutionary histories are well understood (Pinaceae, Proteaceae, Fabales, Restionaceae, and Liliales and other soft-leaved clades). If we can establish that fire-related traits are ancestral (primary) then this would give a pre-emptive role for fire in the evolution of these clades and hold promise that it might apply more generally among seed plants. This would relegate other selective agents to a secondary adaptive role in promoting the evolution of further novel traits in more recent times.

2. Methodology

Ability to address the issue of the relative onset of particular traits within a lineage has only become feasible over the last decade with the introduction of Bayesian trait assignment techniques applied to dated molecular phylogenies (Simon et al., 2009; Bytieber et al., 2011; Crisp et al., 2011; He et al., 2011, 2016). The approach involves reconstructing and dating a molecular phylogeny using DNA sequences and fossils as internal calibration points (Drummond and Rambaut, 2007), and reconstructing the ancient state of a trait at each internal node based on the dated phylogeny and a trait matrix for the extant species assessed. Although there are a few dating approaches, they all incorporate a Bayesian statistical inference framework to estimate divergence times while accounting for the uncertainty in the phylogeny by using a Markov chain Monte Carlo (MCMC) procedure (Pagel et al., 2004). As implemented in the computer package of Pagel and Meade (2006), the Bayesian MCMC method is used to calculate the posterior distributions of likelihood probability of the ancestral states at each internal node of the phylogeny taking into account the uncertainty level at each node. Alternatively, the computer software of Maddison and Maddison (2018) offers options of ancestral trait reconstruction using a parsimonious or maximum likelihood approach.

The trait of interest (or fire-proneness in a separate analysis) is taken to originate in time when the probability of its presence first exceeds the probability of its absence at a dated node. The trait is conserved when a new lineage arises at a node but the targeted trait remains intact (there is no significant probability change). Fire-proneness is treated as an environmental trait assigned to each taxon and its ancient state too can be reconstructed using the above methods. Alternatively, fire-proneness can be treated as a habitat character and reconstructed following the framework of historical biogeography using computer software (Yu et al., 2015). We searched the literature for dated phylogenies for families and genera to which the origin of at least two traits (two fire-related, or one fire-related and one non-fire-related) had been assigned or could be estimated. We supplemented these with our own unpublished assignments on published chronograms (Haemodoraceae, Cistaceae, Fabales). We recorded the age when the lineage first acquired each trait of interest and the likely selective agent (Lamont and He, 2017a) and, if the initial trait was lost or replaced, when and under what conditions.

Recent paleontological discoveries have provided independent corroboration of the results of ancestral trait assignment and the prevailing fire conditions using the above approaches. Carpenter et al. (2015) examined pollen with an affinity to the Proteoid Proteaceae in central Australia from deposits 75–70 Ma and showed that charcoal was indeed abundant then, supporting the conclusion of Lamont and He (2012) that soil and on-plant seed storage had evolved in the Proteoideae as a response to fire by 74 Ma. Similarly, Falcon-Lang et al. (2016) discovered the oldest pine fossil known, dated at 140–131 Ma, and showed that it was often preserved as charcoal, which supports the Bayesian conclusion that *Pinus* was fire-prone at the time of its estimated origin, 126 Ma, and fire-adapted via thick bark (He et al., 2012). More recently,

Table 2
Time of origin (to nearest 1 My) of fire-related* and non-fire-related traits in *Pinus*. [(*)] = exaptation to fire (flammability trait). Times updated using oldest (charcoalified) fossil (131 Ma) from Falcon-Lang et al. (2016). Advent of traits in green postdate the time when pines were first fire-prone and produced fire-resistant bark (> 15 mm thick).

Trait	*Pinus*	Subgenus *Pinus*	Subgenus *Strobus*	Reference
Ectomycorrhizas	> 131	113	113	Strullu-Derrien et al., 2018
Branch retention	> 131	81*	113	He et al., 2012
Fascicles of needle leaves[(*)]	131	113	113	Falcon-Lang et al., 2016
Resin ducts[(*)]	131	113	113	Falcon-Lang et al., 2016
Habitat fire-prone*	131	113	113	Lamont and He, 2017a
Thick bark (> 15 mm)*	131	113	113	He et al., 2012
Thicker bark (> 30 mm)*	113	113	27	He et al., 2012
Serotiny*	113	113	absent	He et al., 2012
Branch shedding*	113	113	10	He et al., 2012
Host for dwarf mistletoes	< 75	< 75	< 75	Vidal-Russell and Nickrent, 2008
Habitat fire-free	65	50	65	Lamont and He, 2017a
Thin bark (< 15 mm)	65	50	65	He et al., 2012
Wingless seeds	46	23	46	this paper (Fig. 2)
Grass stage*	29	29	absent	He et al., 2012
Resprouting*	15	15	absent	He et al., 2012

Mays et al. (2017) discovered fossilised conifer reproductive structures that resemble modern serotinous cones and were consistently associated with charcoal-rich deposits from the Cenomanian (99–94 Ma). He et al. (2012) reported that this reproductive strategy emerged among *Pinus*, the conifer genus with the highest number of extant serotinous species, during the mid-Cretaceous, ~ 90 Ma.

2.1. Pinaceae

Consider the origin of *Pinus* ˜135 million years ago (Ma) that macrofossils and ancestral assignment techniques show coincided with the presence of needle leaves, resin ducts, ectomycorrhizas, ground surface fires and thick bark (Table 2). Bundles of semiterete, isolateral leaves with dense tissues, sunken stomates, thick cuticle and vertical orientation appear to be adapted to drought and temperature extremes, including freezing conditions. However, at this time, temperatures, atmospheric oxygen (O_2) and carbon dioxide were at their highest levels for 350 million years (My) (He et al., 2012) indicating that extremely hot, wet and humid climates prevailed, perhaps with some seasonality in the mid-latitudes. By contrast, surface (mild) fires were abundant, promoted by the high O_2, fuel levels and temperatures independent of seasonality (He et al., 2016) and charcoalified pine wood has been identified at this time (Falcon-Lang et al., 2016). Further, Bayesian assignment techniques have shown that the environment of pines was fire-prone throughout the Cretaceous, initially as surface fires of low intensity (He et al., 2012). Thus, thick bark (> 15 mm) would have been adaptive for plants to survive fire around their bases right from the time of their origin.

This raises the issue of what agents of selection promoted the concurrent evolution of needle leaves and resin ducts? Leaves with an equivalent anatomy have been associated with nutrient-impoverished soils as well as seasonal drought (Lamont et al., 2015) so perhaps these types of habitats, which would also have been especially prone to recurrent fire, could be colonized preferentially by pines? The abundant resins in the leaves (and especially the stems) may have an antiherbivore function but resins and aciculation with low moisture content and vertical orientation also increase their flammability so there may still be an historic link with fire. Certainly, other trait innovations, such as even thicker bark (> 30 mm) coupled with branch shedding, serotiny (cone seed storage) coupled with branch retention, resprouting after crown destruction by fire, and bunching of heat-protective leaves around the apices of young plants (the 'grass' stage) were much later developments (Table 2). These coincided with intensified fire that could now reach the tree crown (He et al., 2012) or possibly savanna-type climates in the case of grass juveniles where frequent fire increased the

risk of recruitment failure. The key role of fire in the evolution of these traits is demonstrated by the delay or absence of their appearance in the fitfully or non-fire-prone subgenus *Strobus* compared with the almost universally fire-prone subgenus *Pinus* (Table 2).

The origin of specialized traits unrelated to fire varies greatly. It is clear that ectomycorrhizas predate the origin of *Pinus* as they are a feature of the Pinaceae generally, crown > 230 Ma (Strullu-Derrien et al., 2018). This gives further support to poor soils vying with fire as key selective agents (Table 1) while their frequent co-occurrence may even have a causal relationship: poor soils induce flammable traits and fire gradually depletes soils of essential nutrients (Archibald et al., 2017; Wittkuhn et al., 2017). Pines as suitable hosts for dwarf mistletoes (*Arceuthobium*, Viscaceae) had to await the separation of the Viscaceae from the Amphorogynaceae, 75–70 Ma (Vidal-Russell and Nickrent, 2008). Because host-specificity is high (Hawksworth and Wiens, 1996) certain *Arceuthobium* species have probably existed only since the origin of their particular host *Pinus* species < 30 Ma. Vulnerability to fire seems to have had little impact on host preferences as subgenus *Pinus* is subject to even more dwarf mistletoe species than subgenus *Strobus* (Hawksworth and Wiens, 1996). As some species migrated into higher (subalpine) altitudes and semi-arid environments during the Cenozoic, their habitats became fire-free and they developed much thinner bark that was less likely to protect the cambium from (unlikely) heat damage.

The evolutionary history of wingless seeds is of particular interest (Fig. 2). *Pinus* was initially fire-prone but non-serotinous (seeds are released as soon as they are ripe). By 113 Ma, subgenus *Pinus* remained fire-prone (81% of extant species) but either retained its seeds on the tree (37%, with old branch retention – otherwise the cones would be lost, and -this also ensured flames reached the crown) or remained non-serotinous (63%, some with branch shedding that reduces flammability of the tree, or experienced only surface fires such that sufficient heat would not reach the cones to stimulate seed release) (He et al., 2012; Lamont and He, 2017a). Six species whose immediate ancestor was serotinous lost serotiny on entering fire-free habitats over the last 25 My. Four retained their wings, one became wingless (*P. pinea*) and another has 20-mm long, ovoid, 2-mm-thick-walled seeds (typical of wingless species that are dispersed by birds) with dehiscent wings (*P. sabiniana*). Subgenus *Strobus* remained largely fire-free (78% of species) and no species developed serotiny. Wingless seeds (50% of extant species) began to evolve in fire-free habitats (Tomback and Linhart, 1990) from 46 Ma.

The impetus for the evolution of wingless seeds may have been the ineffectiveness of wind dispersal in non-fire-prone habitats. It is difficult to view cones rolling down slopes (seeds tend to be retained after
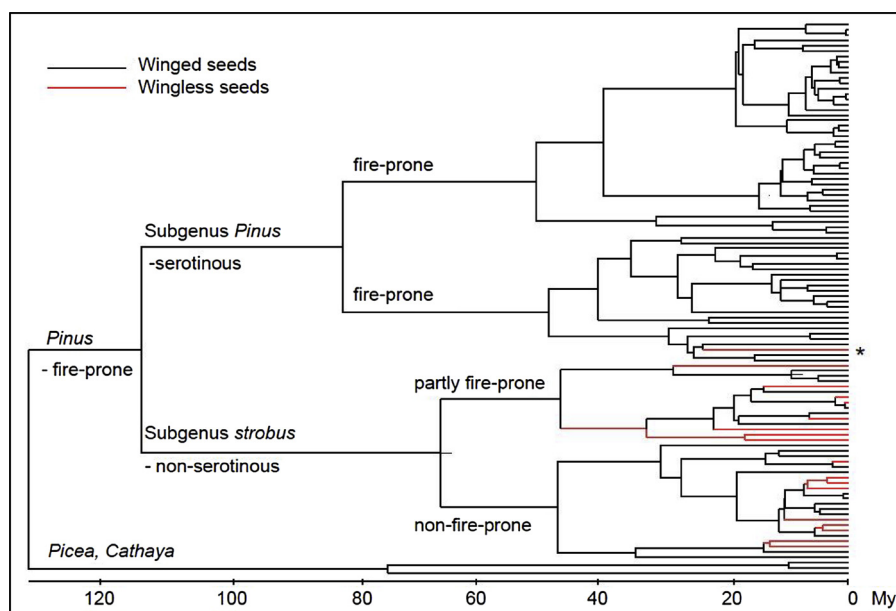
Fig. 2. Chronogram for *Pinus* (updated from He et al., 2012 with a new fossil age for *Pinus* in Falcon-Lang et al., 2016). This shows that *Pinus* arose in a fire-prone environment with fire-resistant bark that split into subgenus *Pinus* that remained fire-prone and gained serotiny, and subgenus Strobus that became fitfully fire-prone and remained non-serotinous. Since winged seeds are beneficial among serotinous cones the evolution of wingless seeds (animal-dispersed) was suppressed. Wingless seeds (data from Tomback and Linhart, 1990) were eventually promoted in several *Strobus* lineages in non-fire-prone habitats where wind-dispersed seeds did not have the same advantages as wingless seeds buried by vertebrates.

scale flexing) as achieving significant distances but cones and seeds are water buoyant and long-distance dispersal via streams is known (Bill et al., 1999). Squirrels and other rodents (Sciuromorphs) may disperse wingless seeds to a limited extent (Vander Wall, 1997) and were evolving 70 Ma, though whether in the presence of pines is unclear (Montgelard et al., 2008). The main dispersers are nutcrackers and jays (Corvidae) though they only spread to Asia from Australia ˜40 Ma and later to N America (Ericson et al., 2005) so cannot have been the initial driver for winglessness. However, their apparent mutualism with pines (Tomback and Linhart, 1990) could apply to the majority of extant species as these originated < 20 Ma (Fig. 2). This must have started as an opportunistic exploitation by the corvids but become an adaptation over time from the perspective of the pines (wing loss, larger seeds, thicker integument, greater dormancy, Greene and Johnson, 1993) and also that of the birds (spatial memory development, larger sublingual pouch size, de Kort and Clayton, 2006). This is a prime example of moderate fire as the pre-emptive evolutionary trigger through initiating a fire-related trait (thick bark) followed by changes in two directions: the development of serotiny in response to more intense fire (subgenus *Pinus*), and the loss of wind dispersal and replacement by wingless, vertebrate-dispersed seeds in the absence of fire (subgenus *Strobus*).

2.2. Proteaceae

In trying to disprove a possible pre-emptive role for fire, Bayesian techniques could be used to trace back lineages whose extant species are currently confined to particular climate types in order to identify when such a climate arose on the chronogram. This might well show that exposure to a particular climate is as equally ancient as fire-prone habitats (Lamont and He, 2017a) in accounting for certain traits. This approach was adopted by Onstein et al. (2016) using 'open' and 'closed' vegetation as the traits of interest where the critical agent of selection was assumed to be seasonal drought acting on leaf size in the Australian Proteaceae. However, 'open' is not in itself a selective agent but a description about the appearance of the vegetation. It is a euphemism for many possible environmental constraints on height and density of plant cover, including high sunlight exposure, nutrient-impoverished or shallow soils, low rainfall or summer-drought/heat, and (especially) frequent fire. Thus, while we can be confident that if extant species in a lineage are fire-prone then their immediate ancestors also were, 'open' is too multicausal to know exactly what that would imply for the ancestral environment.

Onstein et al. (2016) concluded that the Proteaceae radiations in Australia were associated with the seasonal climate of an open Mediterranean-type vegetation. However, Lamont and He (2017b) have shown that such a climate has historically been limited to the west side of the continent (or east of Eyre Peninsular in the case of SE Australia) and was only widespread from the early Miocene. Further, which aspect of 'open' is actually critical for the presence of a taxon in that particular vegetation type? Onstein et al. (2016) made no mention of fire for example, yet 95% of the area occupied by Proteaceae species is highly fire-prone and if they did not possess fire-adapted traits there they would (still) be confined to closed rain and vine forests around the north and east margins of Australia (Fig. 3). All species in sclerophyll vegetation, which is often woodland or forest (https://avh.chah.org.au) that cannot in fact be described as 'open', possess some form of seed storage that depends on fire for their release and/or germination which ensures successful recruitment in the immediate postfire environment, and the presence of such traits in the Proteaceae can be traced to the late Cretaceous (Lamont and He, 2012).

However, unlike fire, where the effects on plant survival, fecundity and distribution are clear, we do not know the growing condition limits for each species in the absence of translocation or distribution-modelling studies. Whenever translocation studies are undertaken, the current distribution is shown to be a subset of the climatic range in which it
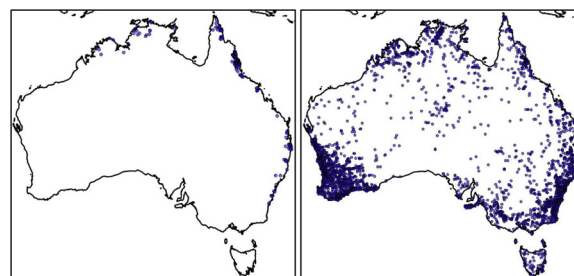
Fig. 3. The distribution of Proteaceae in Australia in relation to fire-proneness. Left: genera in non-fire-prone (rainforest and vine forest) vegetation. Right: genera in fire-prone (savanna grassland, sclerophyll shrubland, woodland and forest) vegetation. Prepared from Australia's Virtual Herbarium, omitting detected outliers, duplicates and cultivated plants and restricted to most abundant genera in each category as program only allows 15 genera to be run simultaneously (https://avh.chah.org.au, 16 May 2017). Note that the continent is 3900 km at its widest. From He and Lamont (2018).

could occur (Witkowski and Lamont, 2006; Araújo and Peterson, 2012). This lack of fixity invalidates using the chronogram approach for ancestral trait assignment in the case of apparent climate-response traits as there is no evidence that a) a species is where it is solely because it is confined to that particular climate, b) a given trait is solely a response to a particular climate, in the absence of definitive comparative experiments, nor c) the trait provides a fitness advantage in those climates compared with ancestral or alternative traits (Lamont and He, 2017b). In fact, the distribution of a species is controlled by many factors other than climate that may take precedence, such as substrate, fire regime, age of its lineage, level of competition from co- occurring species, migration potential, and plant-animal interactions (Perry et al., 2009; Lamont et al., 2016; Pausas and Lamont, 2018).

If one is going to use structural traits to imply past growing conditions then the challenge is to use traits whose relationship, say with drought, is well established (Lamont and He, 2017b). The problem with using leaf size is that small leaves can be due to extended summer drought, low or high temperatures, low aseasonal rainfall, and/or nutrient impoverishment. Furthermore, periodic drought that could induce structural leaf changes in the Proteaceae (Lamont et al., 2002), such as a reduction in leaf size, is essentially a Neogene phenomenon associated with general cooling of the Earth's surface (Zachos et al., 2008). Fire-proneness arose among the Proteoideae about 90 Ma and some form of seed storage with fire-stimulated release/germination is evident 10 My later (Lamont and He, 2012). In the 90–70-My period, whatever the causes of sclerophylly (response to poor soils, seasonal drought or herbivores, Lamont et al., 2002), several scleromorphic, isolateral-leaved clades (Conosperminae, Petrophileae, *Franklandia*) became firmly established. Seasonality would have been limited in duration and distribution in the hot and wet mid-late Cretaceous and would have postdated high O_2 as the chief controller of flammability during the early evolution of sclerophyllous Proteaceae (Lamont and He, 2012; He and Lamont, 2017).

There are numerous independent sources of evidence for the long history of fire in Australia, including phylogenetic studies (He et al., 2011; Crisp et al., 2011; Rundel et al., 2016) and fossil records (Pole and Douglas, 1999; Macphail and Stone, 2004; Carpenter et al., 2015); these suggest that fire was sufficiently frequent and predictable to act as a selective agent by the mid-upper Cretaceous. Thus, the early diversification of Proteaceae is likely to have been strongly linked to the long history of fire in its habitats, not just by their climate and soil characteristics. The ancestral assignments undertaken on *Banksia* and *Hakea*, whose fire- and drought-related traits are well understood, make it clear that their fire responses pre-empted their drought responses (Table 3). Proteaceae without fire (Onstein et al., 2016; Prentice et al., 2017) would still be confined to the rainforest fringe of Australia (Fig. 3) and depauperate in species instead of the dominant position the family currently occupies throughout the continent.

The primeval position of moderate fire on the evolution of the entire Proteaceae continued into the Cenozoic (Table 3). Thus, serotiny was followed in time by dead leaf retention, appearance of the prostrate growth form, and linear, ericoid leaves in *Banksia* 23–16 Ma, possibly associated with intensified fire and/or summer drought linked to the entrenchment of a Mediterranean-type climate in SW Australia by then (Lamont and He, 2017b). In a similar way, resprouting in *Hakea*, possibly linked to a highly variable fire frequency at first, was followed within 4 My by the evolution of large, red inflorescences bearing cyanogens, highly sclerophyllous, terete, spiny leaves and large, woody follicles in response to the advent of bird pollinators/florivores/granivores (Hanley et al., 2009; Lamont et al., 2016). In *Protea*, nonsprouting was followed by resprouting at shorter fire intervals especially in the summer-rainfall region accompanied by the loss of serotiny (Lamont et al., 2013), while winter-dormant buds became a feature of species adapted to the frost-prone uplands of southern/central Africa that became increasingly prominent in the Pliocene/Quaternary (Lamont et al., 2017). As far as adaptations to nutrient-impoverished soils are

concerned, proteoid root clusters are absent from the primitive, fire-prone Symphionematoideae but universal in the sister Proteoideae. This implies that fire may even have preceded poor soils as the key selective agent during the family's early escape from the closed forests of its ancestors. However, this pattern is not repeated in the Grevilleoideae, with fire tolerance a later development among basally rainforest clades (Lamont and He, 2012).

2.3. Fabales

Hard-seededness in the Fabales increases fitness manyfold in fire-prone environments by enabling stored seeds to germinate in response to fire heat at a time when conditions for seedling recruitment are optimal. It has now been established that hard seeds are historically linked to the presence of fire-proneness in several families (Lamont and He, 2012; He et al., 2016) and we collated the literature to show that it is ancestral in the Fabales as well (Fig. 4). The basal Polygalaceae and Caesalpinioideae lack nodules so that nitrogen fixation is essentially confined to the more advanced subfamilies, Mimosoideae and Faboideae, and advanced genera, especially *Chamaecrista*, in the Caesalpinioideae. Sprent (1994) postulated that autotrophic rhizobia gradually invaded their surface roots as legumes moved into drier habitats. Thus, adaptation to soils that are not otherwise sufficiently fertile to meet their nitrogen requirements is a later innovation than fire-stimulated germination, as all Polygalaceae and Caesalpinioideae are hard-seeded (Table 3, Gunn, 1991). Some advanced genera, such as *Mariosousa* and *Pisum*, have lost the hard-seededness of their ancestors as their habitats are no longer fire-prone but retained the ability to fix nitrogen as growth is still nutrient-limited.

Some hard-seeded legumes with dorsiventral bipinnate leaves as the ancestral condition (especially section Mimoseae) have evolved isobilateral phyllodes (expanded petioles) many becoming acicular as the most advanced condition, especially among Australian acacias, that suggest a response to increased aridity (Bouchenak-Khelladi et al., 2010; Lamont and He, 2017b, Table 3). A few acacias and other Fabaceae (e.g., *Daviesia* with fire-stimulated resprouting) have developed phylloclades or even truly leafless cladodes in mediterranean climates (Cook et al., 2015). Some hard-seeded legumes (*Templetonia*, Mirbelieae, Bossiaeeae) evolved red, bird-pollinated flowers, with the *Leptosema* clade oldest at 35 Ma (Toon et al., 2014). *Daviesia epiphylla*, arising 10–5 Ma, has both phylloclades and bird-pollinated flowers (Groom and Lamont, 2015). In passing, the hard-seeded Cistaceae arose 42 Ma with karyotype change associated with changes in flower structure occurring since diversification began 28 Ma (probably due to the presence of new pollinators), and loss of hard-seededness among *Helianthemum* species in non-fireprone habitats beginning 4 Ma (Pérez-García and González-Benito, 2006; Olano et al., 2011; Martínez-Duro et al., 2012; Aparicio et al., 2017; Heckenhauer et al., 2017).

2.4. Restionaceae

The wire-rushes, Restionaceae, can be traced to 101 Ma (Litsios et al., 2014). Rhizomes are universal in this clade although only those placed more deeply in the soil guarantee resprouting in response to fire (Meney and Pate, 1999). Nonsprouters are much better represented in the Cape than in Australia. Fire-stimulated (essentially smoke) germination is probably universal in the Restionaceae (He et al., 2016; Lamont and He, 2017a) so the continental disparity in fire responses must be due to other factors. We attribute the greater incidence of resprouting restios in Australia to a more intense fire history there rather than to subdued landscapes disfavoring the evolution of nonsprouters compared with the Cape as concluded by Litsios et al. (2014). In support, collation of many adaptive traits for 40 genera in the flora of the Mediterranean Basin has shown that the diversification of nonsprouters there can be attributed solely to fire-stimulated germination of their soil-stored seeds and that altitudinal variation was irrelevant (López-

Table 3

For clades predominantly present in fire-prone vegetation, the relative timing of traits adapted to fire as the environmental cue is compared with the onset of traits induced by non-fire-related factors. This shows that moderate fire is ancestral in the time sequence (trigger 1) and that subsequent traits are a response to more or less severe fire or no fire, or to other agents of selection that appeared later (trigger 2). ? indicates a postulated cause but without convincing evidence in support at present.

Clade	Early trait	Trigger 1	References	Later trait	Trigger 2	References
Pinus (Pinaceae)	ability to survive in a fire-prone habitat	presence of recurrent fire	He et al., 2012	ability to survive in a non-fire-prone habitat	absence of fire	Lamont and He, 2017a
Pinus (Pinaceae)	ability to survive in a fire-prone habitat	presence of recurrent fire	He et al., 2012	substrate for host-specific dwarf mistletoes (Arceuthobium, Viscaceae)	separation of Amphorogynaceae, presence of Pinus spp. as suitable aerial hosts	Vidal-Russell and Nickrent, 2008, Nickrent et al. 2010
Pinus (Pinaceae)	thick bark (> 15 mm)	surface fire	He et al., 2012	thicker bark (> 30 mm), greater fire tolerance	crown fire	He et al., 2012
Pinus (Pinaceae)	thick bark (> 15 mm)	surface fire	He et al., 2012	thinner bark (< 15 mm) e.g., P. mugo, P. uncinata	not fire-prone	He et al., 2012; Lamont and He, 2017a
Pinus (Pinaceae)	non-serotinous	surface fire	He et al., 2012	serotinous (+ dead branch retention)	crown fire	He et al., 2012
Pinus (Pinaceae)	serotinous	crown fire	He et al., 2012	wingless seeds (bird dispersed)	migration to fire-free habitats	Tomback and Linhart, 1990; this paper
Pinus (Pinaceae)	interfire recruitment, nonsprouting, limited fire resistance	fire intervals exceed plant longevity	He et al., 2012	resprouting, branch shedding, 'grass' juvenile stage (3 traits)	shorter/more variable fire intervals, crown fire	He et al., 2012
Pinus (Pinaceae)	branch shedding	increasing fire intensity	He et al., 2012	branch retention (6 species)	selection for serotiny, or non-fire-prone	He et al., 2012
Pinus (Pinaceae)	resprouting	shorter/more variable fire intervals, crown fire	He et al., 2012	nonresprouting (1 species)	change in fire regime	Lamont et al., 2018
Proteaceae	ability to survive in a fire-prone habitat (all major subfamilies)	presence of recurrent fire	Lamont and He, 2012	proteoid root clusters in older subfamilies (Proteoideae, Grevilleoideae)	phosphorus-impoverished soils	Weston and Barker, 2006
Proteoideae (Proteaceae)	soil seed storage, fire-stimulated germination	recurrent fire with periodic drought	Lamont and He, 2012	elaiosome-bearing fruits (e.g., Leucospermum, Adenanthos, Mimetes)	evolution of ant dispersers, fire intensification?	Lamont and He, 2012
Banksia (Proteaceae)	serotinous, dead floret retention	moderate crown fire	He et al., 2011	dead leaf retention	intensification of fire? poorer soils (nutrient release on burning)?	He et al., 2011; Lamont and He, 2017b
Banksia – section Prostrata	serotinous, dead floret retention	moderate crown fire	He et al., 2011	prostrate habit; thick, erect leaves	summer drought	He et al., 2011; Lamont and He, 2017b
Banksia – section Sphaerocarpa	serotinous, dead floret retention	moderate crown fire	He et al., 2011	vertical, linear, ericoid leaves	summer drought	He et al., 2011; Lamont and He, 2017b
Banksia	serotinous, dead floret retention	moderate crown fire	He et al., 2011	non-serotinous; dead florets deciduous	fire-free habitats (eg B. verticillata), surface fire (eg B. dentata)	He et al., 2011
Hakea (Proteaceae)	ability to survive in a fire-prone habitat	presence of recurrent fire	Lamont et al., 2016	ability to survive in a non-fire-prone habitat	absence of fire, e.g., rock outcrops (H. clavata, H. adnata)	Lamont et al., 2016
Hakea (Proteaceae)	resprouting, few seeds	highly variable fire frequency?	Lamont et al., 2017b	thick, erect, terete leaves	summer drought and heat – clear skies	Lamont et al., 2015, 2016; Groom and Lamont, 2015
Hakea (Proteaceae)	resprouting, few seeds	highly variable fire frequency?	Lamont et al., 2017b	large, red, cyanide-bearing flowers	bird pollinators	Hanley et al., 2009; Lamont et al., 2016
Hakea (Proteaceae)	resprouting, few seeds	highly variable fire frequency?	Lamont et al., 2017b	spiny leaves	herbivores, granivores	Lamont et al., 2016, 2017b
Hakea (Proteaceae)	resprouting, few seeds	highly variable fire frequency?	Lamont et al., 2017b	fruit–leaf mimicry	granivores (beetles, moths, cockatoos)	Lamont et al., 2016; Groom and Lamont, 2015
Hakea (Proteaceae)	resprouting, few seeds	highly variable fire frequency?	Lamont et al., 2017b	large woody follicles	black cockatoo granivores	Lamont et al., 2016
Hakea (Proteaceae)	serotinous	moderate fire intervals, wet winter?	Lamont et al., 2017b	non-serotinous	Not fire-prone – rock outcrops (eg H. clavata)	Lamont et al., 2016, 2017b
Leucadendron (Proteaceae)	seed storage, fire-stimulated release/germination	moderate fire intervals, wet winter?	Lamont and He, 2012; Tonnabel et al., 2014	wind pollination arising from insect pollination	intensified wind?	Welsford et al., 2016

Table 3 (*continued*)

| Clade	Early trait	Trigger 1	References	Later trait	Trigger 2	References
Persoonieae (Proteaceae)	amphistomatous, vertically oriented leaves (indirectly related to fire – implies high light habitat)	open habitats (recurrent fire with periodic drought), especially in SW Australia	Carpenter et al., 2017	hypostomatous, horizontally aligned leaves (certain Paleogene clades, modern *Laurina*, *Lanceolata* groups)	non-fire-prone closed forest	Carpenter et al., 2017
Protea (Proteaceae)	serotinous	moderate fire intervals, wet winter?	Lamont et al., 2013	non-serotinous	short fire intervals, wet summer?	Lamont et al., 2013
Protea (Proteaceae)	resprouting, non-serotinous	short fire intervals, wet summer?	Lamont et al., 2013	winter-dormant buds	frost-prone, upland grasslands	Smith and Granger, 2017; Lamont et al., 2017
Fabaceae	hard-seeded – all 3 subfamilies	recurrent fire with periodic drought	Bouchenak-Khelladi et al., 2010	nitrogen-fixing nodules (Faboideae, Mimosoideae) (still hard-seeded)	nitrogen-impoverished soils	Diabate et al., 2005; Sprent et al., 2013
Fabaceae	hard-seeded	recurrent fire with periodic drought	Miller et al., 2013	non-hard-seeded (loss of viability when heated)	short fire intervals, wet summer?	Daibes et al., 2017
Faboideae (Fabaceae)	hard-seeded perennial	recurrent fire with periodic drought	Cochrane et al., 2002	non-hard-seeded annual – e.g., *Phaseolus*	tropical montane forest (Andes), non-fire-prone	Debouck et al., 1993; Li et al., 2015
Mimosoideae (Fabaceae)	bipinnate leaved (Mimoseae) (also hard-seeded)	recurrent fire with periodic drought	Cochrane et al., 2002	phyllodinous (*Acacia*) (still hard-seeded)	summer drought, reduced rainfall	Bouchenak-Khelladi et al., 2010
Mimosoideae (Fabaceae)	hard-seeded	recurrent fire with periodic drought	Miller et al., 2013	non-hard-seeded – e.g., *Mariosousa*	desert, non-fire-prone	Seigler et al., 2006
Daviesia (Fabaceae)	hard-seeded, simple leaved, resprouter	recurrent fire with periodic drought	Cochrane et al., 2002	leafless cladodes (also a hard-seeded resprouter)	summer drought, reduced rainfall	Cook et al., 2015
Gastrolobium, Bossiaea (Fabaceae)	hard-seeded, small, non-red flowers	recurrent fire with periodic drought	Cochrane et al., 2002	large, red flowers, abundant nectar (still hard-seeded)	bird pollinators	Toon et al., 2014
Cistaceae	hard-seeded	recurrent fire with periodic drought	Guzmán and Vargas, 2009; D. Korczynskyj, T. He, B. Lamont unpubl.	ovule, pollen structure change (e.g., *Cistus*-type, chromosome change) (also hard-seeded), loss of hard-seededness among *Helianthemum* (2 traits)	unknown – possibly associated with new pollinators? Migration to non-fire-prone gypsum outcrops and salt marshes with increasing aridity	Guzmán and Vargas, 2009; Pérez-García and González-Benito, 2006; Olano et al., 2011; Martínez-Duro et al., 2012; Aparicio et al., 2017
Restionaceae (S Africa)	soil seed storage, fire-stimulated germination	recurrent fire with periodic drought	He et al., 2016	Elaiosome-bearing fruits (e.g., *Cannomois, Willdenowia*)	advent of ant dispersers, fire intensification?	Brown et al., 1994; He et al., 2016
Restionaceae (S Africa)	seed storage, fire-stimulated germination	recurrent fire with periodic drought	He et al., 2016	tolerance of new substrate types (mountain wetlands, coastal lowlands)	climate change, advent of new substrate types	Bouchenak-Khelladi and Linder, 2017
Gladiolus with sister genera (Iridaceae)	cormous geophyte – summer dormant, fire-avoiding	summer drought, (moderate fire intervals?)	Valente et al., 2011	modified flower structures	array of pollinator types (birds, flies, butterflies)	Valente et al., 2012
Burchardia (Colchicaceae)	root-tubered geophyte – summer dormant, pyrogenic flowering	periodic drought, moderate fire intervals	Lamont and Downes, 2011; Chacón and Renner, 2014	seasonally fixed phenology	entrenched mediterranean climate (summer drought)	Vaughton and Ramsey (2001)
Drosera (Droseraceae)	tuberous geophyte, pyrogenic flowering (subgenus *Ergaleium*)	moderate–short fire intervals	Lamont and Downes, 2011	'pygmy' growth form, aestivation (section *Bryastrum*)	summer drought	Yesson and Culham, 2006
Haemodoraceae	pyrogenic flowering, insect pollinated	moderate fire intervals, resources maximal after fire	He et al., 2016	sturdy stemmed, colorful flowers with abundant nectar (*Anigozanthos, Blancoa*)	bird pollinators	Keighery, 1980
Haemodoraceae	pyrogenic flowering	moderate fire intervals, resources maximal after fire	He et al., 2016	loss of pyrogenic flowering	a) still resprouts post-fire, b) killed by fire (fire regime change)	He et al., 2016
Scaevola (Goodeniaceae)	ability to survive in a fire-prone habitat	presence of recurrent fire (Australia)	Jabaily et al., 2014	ability to survive in a non-fire-prone habitat	absence of fire (Pacific Ocean rim)	Jabaily et al., 2014
Orchideae/Diurideae (Ochidaceae)	root-tubered geophytes in fire-prone habitats presence of mild fire (Africa, Mediterranean, Australia)	Lamont and He, 2017a; Nauheimer et al., 2018	array of flower structures, 'rewards' and breeding systems, pyrogenic flowering novel pollinators (e.g., male wasps, cleistogamy), intensification of fire	Groom and Lamont, 2015; Lamont and He, 2017a; Nauheimer et al., 2018		
Disa (Ochidaceae)	ability to survive in a fire-prone habitat	presence of recurrent fire (S Africa)	Bytebier et al., 2011	ability to survive in a non-fire-prone habitat	absence of fire (fire-free pockets, S Africa)	Bytebier et al., 2011
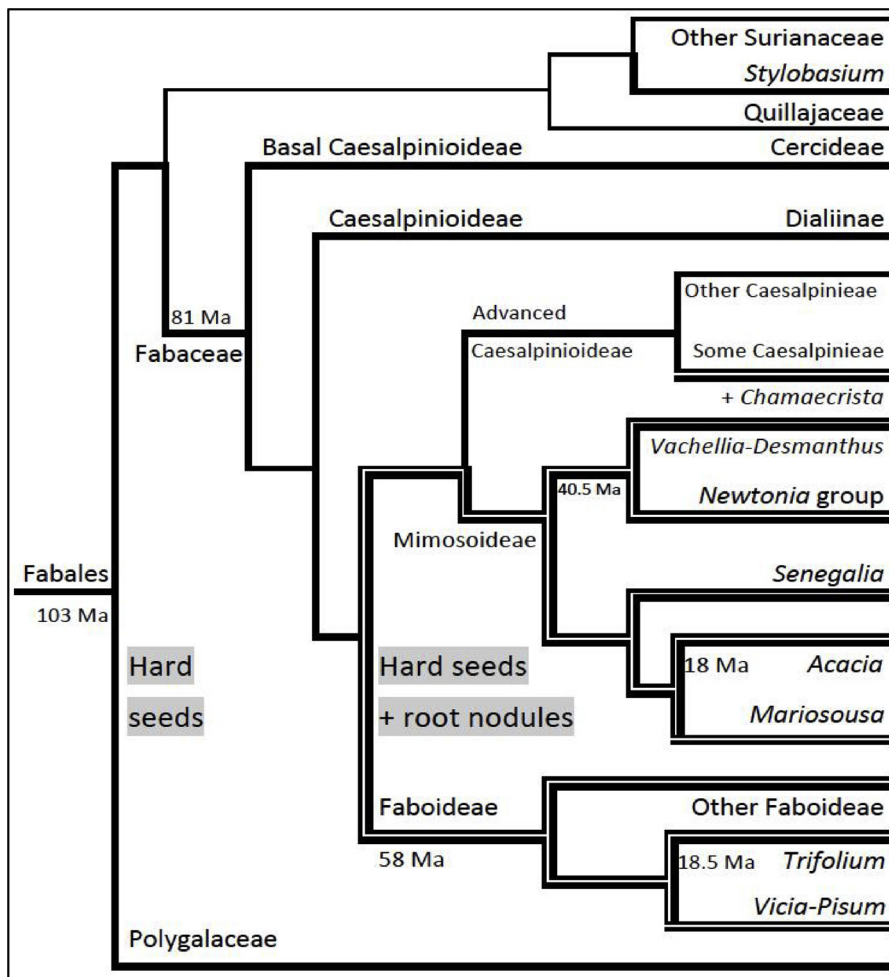
Fig. 4. Phylogeny of the Fabales showing presence (thick lines) and absence (thin lines) of hard-seeded-ness/fire-proneness plus presence of root nodules (double lines) based on ancestral trait-assignment principles. Note that hard-seededness is the ancestral condition in this order with a ˜100-My history, and that the ability to produce root nodules arose at about the time the Faboideae-Mimosoideae clade established 60 Ma. Lineages with soft seeds (*Mariosousa*, *Vicia*, *Pisum*) are non-fire-prone and arose < 20 Ma. Importantly, the basal Caesalpinioideae are hard-seeded but lack nodules. Data for the phylogeny and hard seeds obtained from Gunn (1991); Wojciechowski et al. (2004); Bouchenak-Khelladi et al. (2010); Bello et al. (2012); Sveinsson and Cronk (2014) and Li et al. (2015), and root nodules from Lavin et al. (2001), Doyle (2011); Sprent et al. (2013) and Santos et al. (2017). Adapted from Lamont et al. (2018).

Villalta, 2014). Burial of buds and stem bases not only insulates them from fire heat but also from high summer temperatures especially at the soil surface and reduces desiccation from drought.

The presence of wiry cladodes, with dense, fibrous tissues and leaves reduced to non-photosynthetic scales is universal among restios (Meney and Pate, 1999) and increases their drought/heat tolerances and adaptation to nutrient-impoverished soils via scleromorphy as well as promoting their flammability. High flammability is only adaptive if it benefits some other trait. In this case it probably helps to ensure that at least some seeds receive a sufficient heat pulse for germination. However, there is the problem of confounding between the possible coincident ancestral critical agents of selection: is it fire, poor soils or drought? But, at the time of origin of this clade in the mid-Cretaceous, climatic conditions promoted both growth and fire (high atmospheric O_2, He et al., 2012) so rhizomatous growth is most likely to have been a response to imminent conflagrations. The limited development of ant-attracting arils and pedicels that ensure fruit burial is clearly a later development (He et al., 2016) attributable to the advent of ant dispersers in the Neogene and possibly also to further intensification of fire.

2.5. Liliales and other soft-leaved clades

Just as clades have continued to originate and diversify over the last 100 My or more, so too has the fire regime varied at a given location and biogeographically. Some clades initially evolved in an environment with mild fire at short intervals, others at long or highly variable fire intervals often controlled by the pattern of periodic drought. These early conditions were adequate to induce the evolution of such traits as

moderately thick bark, the geophytic habit often accompanied by pyrogenic flowering, resprouting under conditions where seedling recruitment was unreliable, hard soil-stored seeds or serotiny as adaptive responses (He and Lamont, 2017; Pausas and Ribeiro, 2017; Lamont et al., 2018). However, the ultimate cause of geophyty is unclear. Consider *Gladiolus* (Iridaceae) that arose in the Cape of South Africa 20 Ma (Valente et al., 2011) when periodic fire was now common (He et al., 2016) with annual summer droughts, both associated with the Mediterranean-type climate (MTC) that by this time may have emerged (Rundel et al., 2016). Summer-dormant corms are one way for short-rooted herbs to survive severe periodic drought but also allow them to avoid incineration by summer-autumn fires.

Coupled with geophyty, many *Gladiolus* and its relatives, such as *Watsonia*, show pyrogenic flowering that promotes fecundity (Lamont and Downes, 2011) and implies a long association with fire. The blanket of dead leaves that accumulates over summer-autumn not only fuels the fire that releases nutrients but provides the chemical stimulus (ethylene) for inflorescence inititiation. Other possible life-form options are annuality or evergreenness/nonsprouting combined with deep roots, though fitness for both depends on prolific annual seed production that may well be nutrient-limited here. To what extent fire, rather than seasonality or impoverished soils, was the primary trigger for corm initiation may never be determined. However, it is clear that fire was present at an early stage. Flower modifications as responses to different suites of pollinators (different pollination syndromes) certainly came later than geophyty (Valente et al., 2012). There is a similar problem with *Burchardia* (Colchicaceae) in temperate Australia—tuberous roots (as a possible response to summer drought) and universal pyrogenic flowering might have arisen up to 68 Ma, though diversification began

only 24 Ma (Chacón and Renner, 2014) perhaps in response to intensified fire and seasonal drought due to the advent of a MTC (Rundel et al., 2016; Lamont and He, 2017b). The fixed vegetative phenology (winter-spring) of some *Burchardia* populations is definitely tied to the advent of a MTC (obligate summer dormancy can be viewed as an adaptive response to intensified drought, Vaughton and Ramsey, 2001) and this must be considered a more recent development than geophyty.

Among other geophytic families, diversification of the pyrogenic flowering lineage can be traced to 28 Ma in the carnivorous Droseraceae (subgenus *Ergaleium*) though the basal and sister droseras are nontuberous and therefore are incapable of pyrogenic flowering (Yesson and Culham, 2006; Lamont and He, 2017b, Table 3). The sister 'pygmy' droseras diversified 19 Ma and the tight rosette of 2-mm-diameter leaves among protective basal scales is summer-drought resistant (aestivation). The blood-roots, Haemodoraceae, initiated pyrogenic flowering coincident with their origin, 86 Ma, but this was lost in some genera such as *Shiekia* (rainforests in South America) and *Conostylis* (sclerophyll vegetation in SW Australia) that survives fire, and more recently in *Barberetta* (South Africa, 11 Ma) and most *Anigozanthos* (SW Australia, 7 Ma) that are killed by fire (He et al., 2016). Bird pollination became a feature of *Anigozanthos-Macropidia* with their advent from 12 Ma. Both *Scaevola*, with ant-buried seeds (Goodeniaceae), and *Disa*, with pyrogenic flowering (Orchidaceae), are essentially fire-prone clades and a few of their species migrated into fire-free habitats in more recent times (Table 3). Fire-proneness among terrestrial orchids can be trace back to 60 Ma, and pyrogenic flowering to 50 Ma (Lamont and He, 2017a), while the great array of flower structures, aromas, breeding systems (including facultative cleistogamy) and specialized pollinator operating at the the generic and even individual species levels are much more recent.

3. Discussion

It is clear that the earliest ancestors of modern seed plants, conifers and flowering plants in the upper Lower Cretaceous had stereotypical root systems, stems and fruits/seeds. What is surprising, in the absence of an appreciation of the high levels of productivity and atmospheric O_2, and therefore of fire-proneness, at that time (He and Lamont, 2017), is that, by the early Upper Cretaceous, a wide array of fire-related traits had started to appear among all of these basic plant organs. Such novel traits coincided with, or more usually post-dated, the instigation of fire-proneness as a prerequisite for their assignment as fire-adapted (Lamont and He, 2017a). Only later did other agents of selection appear that directed the evolution of further novel adaptive traits as secondary effects. These can be placed into two groups: a) responses to a change in the fire regime, and b) responses to the introduction of novel agents of selection unrelated to fire. Collating the 47 pairwise comparisons of early traits and their environmental triggers with later traits and their environmental triggers (Table 3) shows that 22 were associated with a change in the fire regime: ten new traits to intensification of fire and 12 to loss of fire-proneness altogether. Intensification was in the form of a change to crown fire, more frequent fire or greater fuel loads. Among clades that are predominantly fire-adapted, it is noteworthy that the absence of such traits, as a response to the rarity of fire, is the advanced condition. Thus, thin bark, opening of fruits at maturity, soft seeds (Fig. 4), wingless seeds (Fig. 1), loss of pyrogenic flowering and hypostomatous (horizontally-aligned) leaves associated with fire-free habitats have evolved more recently from fire-prone ancestors; counterintuitively, they were not the ancestral condition in their clade.

Nine trait innovations can be attributed to a change in climate: seven of these can be attributed to the advent of summer drought due to the establishment of a Mediterranean-type climate (Lamont and He, 2017b), one to greater frost, and one, indirectly, to Neogene cooling creating more lowlands to be colonized by restios (Bouchenak-Khelladi and Linder, 2017). Note that this is the antithesis of the traditional view that fire followed drought, that led to viewing the onset of fire as a recent phenomenon (e.g., compare Bytebier et al. (2011) with He et al. (2016) for contrasting conclusions about the time of origin of fire in the Cape). A change in plant-animal relations was responsible for 12 novel traits: sixof these were due to the introduction of a different class of pollinator (especially birds), one possibly attributable to a greater role for wind as a pollinator, three to increased granivore pressure due to the arrival of black cockatoos in SW Australia (Lamont et al., 2016), and two to the advent of ants as seed dispersers. Two innovations in nutrient uptake were induced by a change in soil properties, essentially due to nutrient depletion. The loss of the need for heat to break dormancy among *Helianthemum*in the Mediterranean Basin is interesting, for certain species during the increasingly dry Quaternary adapted to novel substrates (gypsum outcrop, salt marsh) that are non-fire-prone either because the vegetation is too sparse to support fire or its samphire vegetation is non-flammable (Pérez-García and González-Benito, 2006; Martínez-Duro et al., 2012; Aparicio et al., 2017) Overall, (moderate) fire has been the primary-acting selective agent that has operated over the entire 100 + -My period and other agents acting on non-fire related traits commenced later. A notable exception appears to be mycorrhizal mutualisms that may be as ancient as the origins of roots themselves (Kenrick and Strullu-Derrien, 2014), and highlights the pivotal role played by poor soils and fire in the early history of many plant groups. Above all, non-fire-related traits have arisen from fire-related traits as non-fireprone habitats have become more widespread over time.

In none of the cases involving responses to climate change, the advent of granivores, seed-dispersal agents or potential pollinators, soil-nutrient depletion or presence of new habitats (53% of the 47 cases examined here), did the fire-adapted trait arise later. The fire-adapted trait had previously evolved and then stabilized (Lamont et al., 2013) as it remained essential for maintaining fitness (Fig. 1). These new traits were ancillary to the fire-related one in terms of sequence so that they must be regarded as less fundamental to clade survival. Where the fire-related trait was replaced by another due to a change in the fire regime this shows that adaptive responses to fire (or its absence) have continued to be pivotal for survival. Loss of such traits as thick bark, hard-coated seeds, winged seeds or serotiny demonstrates a) that these traits are only adaptive in a fire-prone environment, b) that there is a fitness cost to that trait in the absence of fire, and c) that this class of traits is finely tuned to the prevailing fire regime. Of course, these temporal patterns only apply to clades that are (or were initially) essentially fire-prone: fire-proneness comes first (trigger 1), then novel fire adaptations evolve (Lamont and He, 2017a), then some other agent of selection arises (trigger 2) followed by novel traits unrelated to the original fire-adapted trait (Table 3). Thus, these secondary triggers may well become primary triggers in non-fire-prone clades. Our survey shows, however, that when the phylogeny of clades with a mixture of fire-prone and fire-free species is explored their origins are found to be fire-prone (Lamont and He, 2017a) and the early fire-adapted traits pre-empt all others.

While current evidence for the ultimate selective agent in the evolution of certain traits may be ambivalent, such as corms in the Iridaceae (Valente et al., 2011), fascicles of needle leaves in *Pinus*, and amphistomaty in the Proteaceae (Carpenter et al., 2017), it is clear that their initiation still coincided with the presence of fire, and that other, non-fire-related, traits arose later. Certainly, part of the problem in distinguishing some sequences is current uncertainty on whether the root or crown node, or some other position along the stem, best indicates the actual time of origin of traits in chronograms (Lamont and He, 2017b). As Bayesian assignment methods improve (e.g., http://blog.phytools.org/2017/04/extracting-positions-of-character-state.html), phylogenies become more complete, extant trait states are better known, and the accuracy of biological clocks (older fossils of known age) improves, so will it be possible to more accurately estimate the actual times of origins of various traits to determine to what extent they really did coincide or were temporally disparate.

Declarations of interest

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